2017-09-18

# Reclassification of Thiomicrospira hydrogeniphila (Watsuji et al. 2016) to Thiomicrorhabdus hydrogenophila comb. nov., with emended description of Thiomicrorhabdus (Boden et al., 2017)

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10.1099/ijsem.0.002279
International Journal of Systematic and Evolutionary Microbiology
Microbiology Society

International Journal of Systematic and Evolutionary Microbiology

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--Manuscript Draft--

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| **Manuscript Number:** | IJSEM-D-17-00400R1 |
| **Full Title:** | Reclassification of Thiomicrospira hydrogeniphila (Watsuji et al. 2016) to Thiomicrorhabdus hydrogenophila comb. nov., with emended description of Thiomicrorhabdus (Boden et al., 2017) |
| **Article Type:** | Taxonomic Description |
| **Section/Category:** | New taxa - Proteobacteria |
| **Keywords:** | Chemolithoautotroph; Thiomicrospira; Thiomicrorhabdus; Hydrogenovibrio; Thioalkalimicrobium; hydrogen |
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| **Manuscript Region of Origin:** | UNITED KINGDOM |
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# Reclassification of *Thiomicrospira hydrogeniphila* (Watsuji *et al.* 2016) to *Thiomicrorhabdus hydrogenophila* comb. nov., with emended description of *Thiomicrorhabdus* (Boden *et al.*, 2017)

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KEYWORDS: Chemolithoautotroph, *Thiomicrospira*, *Thiomicrorhabdus*, *Hydrogenovibrio*, *Thioalkalimicrobium*, hydrogen

RUNNING TITLE: Reclassification of *Thiomicrospira hydrogeniphila* to *Thiomicrorhabdus hydrogeniphila* comb. nov.

ABBREVIATIONS: We have used 3-letter abbreviation convention recommended in Boden *et al.* (2017) for the genera with similar names, *viz*. *Thiomicrospira* (*Tms*.), *Thiomicrorhabdus* (*Tmr*.) and *Thioalkalimicrobium* (*Tam.*), to avoid ambiguity particularly given the recent reclassification.

**Abstract**

The genus *Thiomicrorhabdus* (*Tmr*) in the *Piskirickettsiaceae* in the *Thiotrichales* of the *Gammaproteobacteria* contains four species of sulfur-oxidizing obligate chemolithoautotroph with validly published names, all previously classified as *Thiomicrospira* (*Tms*) species. Here we demonstrate that *Thiomicrospira hydrogeniphila*, a recently published hydrogen-utilizing chemolithoautotroph closely related to *Thiomicrorhabdus frisia* (type species of *Thiomicrorhabdus*) should be classified as a member of the genus *Thiomicrorhabdus* and not *Thiomicrospira*, as *Thiomicrorhabdus hydrogeniphila* comb. nov., on the basis of comparative physiology and morphology as well as 16S rRNA (*rrs*) gene identity of *Tms. hydrogeniphila* MAS2$^T$ being closer to that of *Tmr. frisia* JB-A2$^T$ (99.1 %) than to *Tms. pelophila* DSM 1534$^T$ (90.5 %) or *Hydrogenovibrio marinus* MH-110$^T$ (94.1 %), and on the basis of the topology of 16S rRNA gene maximum likelihood trees, which clearly place *Tms. hydrogeniphila* within the genus *Thiomicrorhabdus*. It was also noted that thiosulfate-grown *Thiomicrorhabdus* spp. can be distinguished from *Thiomicrospira* spp. or *Hydrogenovibrio* spp. on the basis of the 3 dominant fatty acids ($C_{16:1}$, $C_{18:1}$ and $C_{16:0}$), and from other *Thiomicrorhabdus* spp. on the basis of the 4$^{th}$ dominant fatty acid, which varies between the species of this genus – this could provide a useful diagnostic method. We provide an emended description of *Thiomicrorhabdus* [1] to take into account the properties of *Thiomicrorhabdus hydrogeniphila* comb. nov.

The taxonomy and systematics of the genera *Thiomicrospira* (*Tms*), *Hydrogenovibrio* (*H*) and *Thioalkalimicrobium* (*Tam*) were recently revised [1], proposing the genus *Thiomicrorhabdus* (*Tmr*) for a clade of rod-shaped organisms previously classified as *Thiomicrospira* spp., and reclassifying one other clade of *Thiomicrospira* spp. as *Hydrogenovibrio* spp., leaving only *Tms. pelophila* (type species) and *Tms. thyasirae* as *Thiomicrospira* spp., but all four members of *Thioalkalimicrobium* were also reclassified to *Thiomicrospira*. This was based on a polyphasic study of chemotaxonomic, physiological, genomic and phylogenetic elements. Shortly before our study [1] was accepted, *Thiomicrospira hydrogeniphila* [2] was published, based on a eurypsychrophilic hydrogen and sulfur-oxidizing chemolithoautotroph isolated from enrichment cultures inoculated with the slurry of a 10-month old tank of seawater from Toyko Bay, Japan, that had been incubated with a block of beef tallow at 10 °C. Here we present the short case that this species should also be circumscribed into the genus *Thiomicrorhabdus* per all other members of the same clade of *Thiomicrospira* as proposed by Boden *et al.* [1], as *Thiomicrorhabdus hydrogeniphila* comb. nov., and we accordingly revise the description of *Thiomicrorhabdus* [1] to take into account the properties of this species.

*Thiomicrorhabdus* [1] comprises four species with validly published names – *Thiomicrorhabdus frisia* [3], *Thiomicrorhabdus chilensis* [4], *Thiomicrorhabdus arctica* [5] and *Thiomicrorhabdus psychrophila* [5]. All were isolated from marine sediments and can use thiosulfate and other reduced sulfur species as electron donors but none have been found to use molecular hydrogen thus far. *Tmr. psychrophila* and *Tmr. arctica* are stenopsychrophilic, whereas the other two species are eurypsychrophilic and have more mesophilic temperature optima. All species are moderate halophiles requiring 40 – 100 mM sodium chloride (2.3 – 5.8 g/L) for growth, with optima of 250 – 400 mM (14.6 – 23.4 g/L). *Thiomicrorhabdus* spp. share the same 3 dominant fatty acids (palmitoleic ($C_{16:1}$), vaccenic

($C_{18:1}$), palmitic ($C_{16:0}$) acids) when grown on thiosulfate agar plates, but can be easily distinguished by their next-dominant fatty acid (*Tmr. chilensis*, stearic acid ($C_{18:0}$); *Tmr. arctica*, myristoleic acid ($C_{14:1}$); *Tmr. psychrophila*, lauroleic acid ($C_{12:1}$)). The G+C contents of genomic DNA range from 39.6 to 49.9 mol%.

We have shown previously [1] that the 16S rRNA gene phylogeny reliably supports those of the *recA* and *gyrB* genes and of more complex analyses using 53 ribosomal protein genes (rMLST, [6]). In the absence of a genome sequence for *Tms. hydrogeniphila*, we are limited to the 16S rRNA gene here for phylogenetic analyses, but are confident from our previous study of this group of genera that this gene indeed accurately reflects the phylogeny using more genes. Gene sequences of this clade of organisms were curated from the GenBank™ database and aligned using the MUSCLE algorithm [7] in MEGA 7.0.2 [8]. A maximum-likelihood tree (Figure 1) was built using the Tamura-Nei model [9]. Bootstrap values at nodes represent 5,000 resamplings of the tree, and are shown where greater than or equal to 70 %. It can be seen from Figure 1 that *Tms. hydrogeniphila* falls within the genus *Thiomicrorhabdus*, which is further supported on the basis of the 16S rRNA gene identity to *Tmr. frisia* (type species) of 99.1 %, *versus* 90.5 % to *Tms. pelophila* and 94.1 % to *H. marinus*. These data indicate that *Tms. hydrogeniphila* is not the same genus as either *Tms. pelophila* or *H. marinus* on the basis of the proposed genus cut-off of 94.5 % identity ("the Yarza cut-off" [10]), and on the basis of tree topology. It is worth noting that *Tms. hydrogeniphilus* was robustly demonstrated by Watsuji *et al.* [2] to be distinct from *Tmr. frisia* on the basis of DNA-DNA hybridisation, thus we regard it as a distinct species. We have also previously demonstrated [1] that the other species of *Thiomicrorhabdus* (and *Hydrogenovibrio* and *Thiomicrospira*) are also correctly circumscribed on the basis of *in silico* DNA-DNA hybridisation scores.

Differential properties of *Tms. hydrogeniphila versus Thiomicrospira sensu stricto*, *Hydrogenovibrio* and *Thiomicrorhabdus* spp. are curated in Table 1. It can be seen that the cell size, morphology, maximum specific growth rate on thiosulfate, motility and flagellation are more similar to *Thiomicrorhabdus* spp. rather than to *Thiomicrospira* spp. or *Hydrogenovibrio* spp. The temperature range and optimum for *Tms. hydrogeniphila* are very similar to the nearest neighbour in terms of the 16S rRNA gene, *Thiomicrorhabdus frisia* (type species). The dominant three fatty acids of *Tms. hydrogeniphila* are identical to all *Thiomicrorhabdus* spp. but fall in a different order to *Thiomicrospira* and *Hydrogenovibrio* spp. The fourth-dominant fatty acid is lauric acid ($C_{12:0}$), which is distinct from the other *Thiomicrorhabdus* spp. and could provide a means to diagnose speciation with rapidity since all species differ in this fourth dominant acid. The G+C content of genomic DNA is identical to *Tmr. frisia*, but as already stated, it has been distinguished from this species on the basis of DNA-DNA hybridisation previously, however, future *in silico* DNA-DNA hybridisation studies once the genome sequence is complete will be needed to confirm this since both the G+C content and 16S rRNA gene identity with *Tmr. frisia* are very high, yet the DNA-DNA hybridisation percentage of Watsuji *et al.* [2] is still below 20 %, which appears rather low. *Tms. hydrogeniphila* can use molecular hydrogen as an electron donor, which is distinct from all *Thiomicrorhabdus* spp., and this warrants the emending of the genus description to add this property, which is found in some *Hydrogenovibrio* spp., but not in this genus.

We conclude that *Thiomicrospira hydrogeniphila* actually represents a member of the recently defined genus *Thiomicrorhabdus* (composed entirely of former *Thiomicrospira* spp.) and propose the name *Thiomicrorhabdus hydrogeniphila* comb. nov. to reflect this. We also propose some minor revisions to the Boden *et al.* [1] description of *Thiomicrorhabdus* to take into account the properties of *Tmr. hydrogeniphila* comb. nov. and other data from Watsuji *et al.* [2].

**Emended description of *Thiomicrorhabdus* (Boden *et al*. 2017)**

*Thiomicrorhabdus* (Thi.o.mi.cro.rhab'dus. Gr. n. *theion*, L. transliteration *thium*, sulfur; Gr. adj. *mikrós*, small; Gr. fem. n. *rhabdos* , N.L. transliteration *rhabdus*, rod or wand. N.L. fem. n. *Thiomicrorhabdus*, small sulfur-oxidising rod).

Gram-stain-negative. Cells when grown in liquid media are rod-shaped. Typical cell lengths are 0.8 – 2.7 μm and diameters are 0.3 – 0.6 μm, wider than *Thiomicrospira* spp. Do not form endospores or exospores. Use molecular oxygen as the sole terminal electron acceptor. Have a $cbb_3$-type cytochrome *c* oxidase (EC 1.9.3.1). Form white to yellow, entire colonies on thiosulfate-agar, coated in small granules of elementary sulfur. Motile, cells are monotrichous when grown in liquid media. Obligately chemolithoautotrophic with heterotrophy never observed. Can use thiosulfate, tetrathionate or sulfide as sole electron donors and at least one species uses molecular hydrogen, but none are known to use thiocyanate, sulfite, iron or manganese. Some species can use elementary sulfur as a sole electron donors. Fix carbon dioxide *via* the transaldolase-variant Calvin-Benson-Bassham cycle. All species use ammonium as a nitrogen source. Does not fix dinitrogen. No nitrogenase genes observed in genome sequences. Has form IAc and/or form IAq, and form II RuBisCo.

All species produce elementary sulfur when growing on thiosulfate at neutrality, but at varying degrees. Never auxotrophic for vitamin $B_{12}$. Growth occurs from pH 4.2 to pH 9.0 but range varies with species – pH optima are pH 6.5 to 8.5. Grows from -2 °C to 42 °C with optima of 11.5 °C to 35 °C, varying by species, most of which are stenopsychrophilic or eurypsychrophilic. NaCl is required for growth, with minima of 40 – 100 mM, maxima of 1,240 mM across the genus and optima of 250 – 470 mM. Does not reduce nitrate to nitrite. G+C fractions of genomic DNA are 39.6 – 49.9 mol%. Dominant respiratory quinone is ubiquinone-8. Dominant fatty acids are palmitoleic ($C_{16:1}$), vaccenic ($C_{18:1}$) and palmitic

($C_{16:0}$) acids, in that order, which is distinct from *Thiomicrospira* spp. and *Hydrogenovibrio* spp., but consistent with other *Thiomicrorhabdus* spp., followed by stearic ($C_{18:0}$) and myristoleic ($C_{14:1}$) acids. Members of the *Piskirickettsiaceae* in the *Thiotrichales* of the *Gammaproteobacteria.*

Type species: *Thiomicrorhabdus frisia* (Basonym: *Thiomicrospira frisia*) [3]

**Description of *Thiomicrorhabdus hydrogeniphila* comb. nov.**

*Thiomicrorhabdus hydrogeniphila* (hy.dro.ge.ni'phi.la. Gr. n. *hydôr*, water; Gr. v. *gennaô*, to beget, to bring forth, to produce; N.L. n. *hydrogenum*, hydrogen, *i.e.* that which produces water; N.L. adj. *philus* from Gr. adj. *philos*, friend, someone dearly loved; N.L. fem. adj. *hydrogeniphila*, hydrogen-loving).

Gram-stain-negative. Cells grown in liquid media are rod shaped and motile by means of a single polar flagellum. 0.9 – 1.8 μm in length and 0.3 – 0.5 μm in diameter. Cells grown in MMJS broth [2] were obligately aerobic, using only molecular oxygen as their terminal electron acceptor and tolerating up to 40 % (*v/v*) oxygen in a gas phase of nitrogen supplemented with 5 % (*v/v*) carbon dioxide as sole carbon source, at atmospheric pressure. Nitrate, nitrite, ferric iron, ferrihydrite, selenate and fumarate are not used as terminal electron acceptors. Obligately chemolithoheterotrophic, electron donors supporting growth are: thiosulfate, tetrathionate, elementary sulfur, sulfide and molecular hydrogen. Sulfite was not used. Oxidation of molecular hydrogen is repressed at high oxygen partial pressures. Ammonium was the sole nitrogen source, and nitrate, nitrite and molecular nitrogen were not used. Selenate, tungstate and vitamins (*viz*. biotin, folate, pyridoxine, thiamine, riboflavin, nicotinate, pantothenate, cyanocobalamin, *p*-aminobenzoate or lipoate) were not required for growth. Growth occurs between 2 °C and 40 °C with an optimum of 30 °C, and between pH 5.0 and pH 8.0 with an optimum of pH 6.0, in MMJS medium incubated under air. Growth

occurs from 30 – 1,380 mM $Na^+$, with optimal growth at 270 mM $Na^+$. Sensitive to ampicillin (50 μg/mL, 143 μM), chloramphenicol (50 μg/mL, 155 μM), , kanamycin A (50 μg/mL, 103 μM), rifampicin (50 μg/mL, 60 μM), streptomycin (50 μg/mL, 86 μM); resistant to vancomycin (50 μg/mL, 35 μM). Heterotrophic or chemolithoheterotrophic growth (the latter with thiosulfate) is not observed on any carbon source tested, *viz*. yeast extract, peptone, tryptone, casein, starch, carboxymethylcellulose or casamino acids (each at 0.1% (*w/v*)); formate, acetate, glycerol, citrate, tartarate, fumarate, malate, succinate, propionate, lactate, oxalate, pyruvate or the 20 structural amino acids (each at 5 mM); glucose, galactose, fructose (each at 1.1 mM); sucrose, lactose, maltose or trehalose (each at 0.6 mM). Maximum specific growth rate on thiosulfate under optimal conditions was 0.4 $h^{-1}$. Dominant fatty acids in thiosulfate-grown cells are palmitic acid ($C_{16:0}$), palmitoleic acid ($C_{16:1}$) and vaccenic acid ($C_{18:1}$). Of the hydroxylated fatty acids, only 3-hydroxycaprylic acid ($C_{10:0}$ 3-OH) is found. Lauroleic ($C_{12:1}$) and myristoleic ($C_{14:1}$) acids are not found, but lauric ($C_{12:0}$) and myristic ($C_{14:0}$) acids are in minor amounts – these 4 acids are diagnostic *versus* other *Thiomicrorhabdus* spp. (*cf*. Table 1). The G+C content of genomic DNA of the type strain is 39.6 mol% (HPLC).

Basonym: *Thiomicrospira hydrogeniphila* Watsuji *et al*. 2016.

Type strain is MAS2$^T$ = JCM 30760$^T$ = DSM 100274$^T$, isolated from enrichment cultures using molecular hydrogen as the sole energy source, inoculated with slurry obtained from a sulfidic tank containing surface seawater from Tokyo Bay, supplemented with a block of beef tallow (*c*. 350g/L), held at 10 °C for 10 months.

**Funding Information**

We thank the Royal Society (UK) for Research Grant RG120444 to RB and the School of Biological and Marine Sciences (University of Plymouth) for the postdoctoral fellowship funding for LPH.

**Conflicts of interest**

The authors declare that they have no competing interests.

**Ethical Statement**

No human or animal experiments were conducted in this study.

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**Figure 1**. Maximum likelihood tree based on the 16S rRNA (*rrs*) gene sequences from *Thiomicrospira hydrogeniphila* MAS2$^T$ and all members of the genera *Thiomicrospira*, *Thiomicrorhabdus*, *Galenea* and *Hydrogenovibrio* with validly published names. The outgroup is the gene sequence from *Halothiobacillus neapolitanus* NCIMB 8539$^T$. Genes were aligned using the MUSCLE algorithm in MEGA 7.0.20 and trees built using the Tamura-Nei model with the nearest-neighbour interchange (NNI) heuristic method and partial deletion of gaps. Topology with the superior log-likelihood is shown, with numbers at nodes representing the percentage of 5,000 bootstrap replicates for which that topology was preserved (values < 70 % are omitted). GenBank™ gene accession numbers are giving in parentheses. Scale bar represents the number of substitutions per site. 1,270 nt were used in the analysis. Type species of genera are emboldened and the test sequence (*Tms. hydrogeniphila* MAS2$^T$) is underlined.

**Table 1**. Comparative properties of *Thiomicrospira hydrogeniphila* MAS2$^T$ with all species of *Thiomicrorhabdus* with validly published names, and conglomerated properties of *Thiomicrospira* and *Hydrogenovibrio*. Data are from [1] or [2].

Values are positive (+), weak positive (±), negative (-) or not determined (*ND*).

Table 1



| | ***Thiomicrorhabdus Hydrogeniphila* MAS2$^T$** | ***Thiomicrorhabdus frisia* JB-A2$^T$** | ***Thiomicrorhabdus chilensis* Ch-1$^T$** | ***Thiomicrorhabdus arctica* SVAL-E$^T$** | ***Thiomicrorhabdus psychrophila* SVAL-D$^T$** | ***Thiomicrospira* spp.** | ***Hydrogenovibrio* spp.** |
|---|---|---|---|---|---|---|---|
| **16S rRNA gene sequence identity to (%):** | | | | | | | |
| *Tms. pelophila* DSM 1534$^T$ | 90.5 | 91.6 | 92.0 | 92.9 | 92.9 | 95.9-100.0 | 92.1-94.4 |
| *Tmr. frisia* JB-A2$^T$ | 99.1 | 100.0 | 96.0 | 96.0 | 96.0 | 90.3-91.4 | 94.2-95.5 |
| *H. marinus* MH-110$^T$ | 94.1 | 94.2 | 94.8 | 94.0 | 94.1 | 91.4-92.9 | 95.7-100.0 |
| **Properties** | | | | | | | |
| Colony colour on thiosulfate agar grown under air | White, cream | White, yellow | *ND* | *ND* | *ND* | White, pink or red | White, cream or yellow |
| Heterotrophic | - | - | - | - | - | - | ± |
| G+C fraction (mol%) | 39.6 | 39.6 | 49.9 | 42.4 | 42.5 | 45.6 – 49.3 | 44.1 – 56.6 |
| Maximum specific growth rate on thiosulfate under optimal conditions ($h^{-1}$) | 0.4 | 0.45 | 0.4 | 0.14 | 0.2 | 0.07 – 0.33 | 0.25 – 0.8 |
| Temperature range (°C) | 2.0 – 40.0 | 3.5 –39.0 | 3.5 – 42.0 | -2.0 – 20.8 | -2.0 – 20.8 | 3.5 – 41.0 | 3.5 – 55.0 |
| Temperature optimum (°C) | 30 | 32 – 35 | 32 – 37 | 11.5 – 13.2 | 14.6 – 15.4 | 25 – 40 | 28 – 37 |
| Dominant fatty acids in thiosulfate-grown cells | $C_{16:1}$ $C_{18:1}$ $C_{16:0}$ $C_{12:0}$ | *ND* | $C_{16:1}$ $C_{18:1}$ $C_{16:0}$ $C_{18:0}$ | $C_{16:1}$ $C_{18:1}$ $C_{16:0}$ $C_{14:1}$ | $C_{16:1}$ $C_{18:1}$ $C_{16:0}$ $C_{12:1}$ | $C_{18:1}$ $C_{16:1}$ $C_{16:0}$ $C_{14:0}$ | $C_{16:1}$ $C_{16:0}$ $C_{18:0}$ $C_{18:1}$ |
| Molecular hydrogen as an electron donor | + | - | - | - | - | - | ± |
| Cell length (µm) | 0.9-1.8 | 1.0-2.7 | 0.8-2.0 | 1.2-1.5 | 1.3-1.7 | 0.8 – 5.0 | 0.8 – 3.0 |
| Cell width (µm) | 0.3-0.5 | 0.3-0.5 | 0.3-0.5 | 0.5-0.6 | 0.5-0.6 | 0.2 – 2.0 | 0.2 – 0.7 |
| Morphology | Rod | Rod | Rod | Rod | Rod | Vibrio, ring, spiral | Vibrio, curved rod |
| Motility | + | ± | + | ± | + | ± | + |
| Flagella | 1 | *ND* | *ND* | 1 | 1 | 0-3 | 1 |

Figure 1

Click here to download Figure 16S tree.pdf